

LEPTODACTYLON PUNGENS SUBSP. *HAZELIAE*
(POLEMONIACEAE), A NEW COMBINATION FOR
A SNAKE RIVER CANYON ENDEMIC

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ABSTRACT

Morphological study of herbarium and living specimens of *Leptodactylon* from the Pacific Northwest and northern Great Basin indicates that the little-known species *Leptodactylon hazeliae* Peck is more appropriately treated as a subspecies of *L. pungens* (Torr.) Rydb. This rare taxon occurs only in the Snake River Canyon of Oregon and Idaho, where it inhabits sheer rock outcrops in *Poa-Agropyron-Purshia* communities. The relationship of subsp. *hazeliae* to other species of *Leptodactylon* is not clear. The subspecies is morphologically intermediate between *L. pungens* and *L. watsonii* (A. Gray) Greene, a trait it shares with the recently described *L. glabrum* Patterson and Yoder-Williams, an epilithic species of northern Nevada and adjacent Idaho. It is speculated that *L. glabrum* and subsp. *hazeliae* may have originated from past hybridization events involving *L. pungens* and *L. watsonii*.

Leptodactylon H. & A. is a small genus of suffrutescent perennials and low subshrubs endemic to western North America (Grant 1959, Cronquist 1984). It is primarily distributed in arid regions east of the Cascade-Sierran axis, but also occurs in the coastal mountains and maritime areas of southern California and adjacent Mexico. Its members are reminiscent of perennial species of *Phlox* and *Linnanthus*, but are distinguished from those genera by the combination of prickly leaves, prominent membranes in the calyx sinuses, and equally inserted stamens.

The generic limits of *Leptodactylon* are relatively well-marked morphologically, but the delineation of species and infraspecific taxa has been historically a source of frustration for students of Polemoniaceae. Several species exhibit considerable phenotypic plasticity, often with patterns of regional variation that are difficult to circumscribe. In the only comprehensive treatment of the genus, Wherry (1945) recognized 10 species and several varieties and forma. Unfortunately, the relationships between morphology and geographic range presented in his account are vague, and the taxonomy has not been readily adaptable for use in state or local floras. Later workers (Davis 1950, Mason 1951, Harrington 1954, Cronquist 1959, 1984, Munz 1959, Kearney and Peebles 1960) reduced the number of accepted species to six or seven and elected to disregard

those proposed by Wherry (1945) that intergrade extensively across broad geographic zones. Some authors advocate the use of infra-specific categories to accommodate these variants. However, in lieu of detailed phytogeographic studies, the application of these names in any given area is largely conjectural.

Most of the variation in *Leptodactylon* is represented in a complex centered around *L. pungens* (Torr.) Rydb., one of three widespread, polymorphic species that range throughout all or much of the Intermountain Region and American Southwest. Fourteen of the twenty *Leptodactylon* taxa recognized by Wherry (1945) are segregates of *L. pungens*, and the species has a lengthy synonymy of over forty nomenclatural combinations dating to the early nineteenth century (Cronquist 1959, 1984). The other two intermountain species, *L. watsonii* (A. Gray) Greene and *L. caespitosum* Nutt., share a number of traits with *L. pungens*, and in some respects the three entities constitute a morphological continuum. Populations of the three species also overlap along an ecological gradient, and may coincide geographically, particularly in the eastern Great Basin and Wyoming. Despite the morphological similarities that imply common ancestry, and the high potential for sympatry, there are no available data to suggest that these species are interfertile. The two characters that typically are used to identify them, i.e., phyllotaxy and the number of flower parts, show remarkable consistency considering the overall variability of the groups. *Leptodactylon caespitosum* and *L. watsonii* are opposite-leaved and have 4-merous and 6-merous flowers, respectively, whereas *L. pungens* has 5-merous flowers and variable leaf insertion, usually with the upper alternate and the lower opposite. In the few cases where 5-merous flowers occur in *L. watsonii* (Cronquist 1984, Meinke pers. observ.), the plants are distinguished from the woodier *L. pungens* on the basis of flexible, subherbaceous flowering stems and opposite leaves throughout, including the inflorescence bracts.

Because of the consistency of the aforementioned differences, it is noteworthy that populations of *Leptodactylon* have been discovered recently that do not fit patterns of variation previously described for *L. pungens* or *L. watsonii*. The plants are located in the Snake River Canyon of northeastern Oregon and adjoining Idaho, a locality rich in disjunct and endemic species (Peck 1961). The most striking features of living specimens of the riverine populations are the short inflorescence branches, the pliable, bright green leaves, and the diurnal flowering that contrasts with the mostly vespertine corolla expansion of other Pacific Northwest *Leptodactylon* taxa.

My preliminary study showed that the plants correspond morphologically with the only known collection of *L. hazeliae* Peck, a taxon described in 1936 from three immature branches gathered

near the Snake River. Subsequent examination of several hundred herbarium specimens of *L. pungens* and *L. watsonii* supports the taxonomic recognition of the Snake River populations based on several minor but constant morphologic traits (Table 1). These plants are apparently ecologically specialized as well, being restricted to the uniquely mild (for the region) climate of the Snake River Canyon. The number of unambiguous characters separating the Snake River plants from other populations of *L. pungens* are fewer than the number distinguishing *L. pungens* from other species in the genus. I propose that these populations be recognized at the level of subspecies, under *L. pungens*. The spelling of the subspecific epithet in the following new combination reflects an orthographic correction from Peck's (1936) original "*Hazelae*", after Recommendation 73C.1b of the ICBN.

Leptodactylon pungens (Torr.) Rydb. subsp. ***hazeliae*** (Peck) Meinke, stat. et comb. nov. (Fig. 1)—*Leptodactylon Hazelae* Peck, Proc. Biol. Soc. Wash. 49:111. 1936; *L. pungens* subsp. *hookeri* (Dougl. ex Hook.) Wherry forma *hazeliae* (Peck) Wherry, Amer. Midl. Naturalist 34:383. 1945.—TYPE: USA, OR, Wallowa Co., dry rocky slope, Snake River Canyon near mouth of Battle Creek, 13 Apr 1934, *Barton s.n.* (Holotype: WILLU 18415!).

Additional specimens. USA, ID, Idaho Co.: Snake River Canyon, ¼ mi downstream from Granite Creek, local on cliffs, 22 May 1974, *Henderson, Wellner, and Bingham 1306* (ID!), two sheets); Snake River Canyon, Suicide Point, on trail near U.S. Forest Service sign, 15 Jun 1978, *Mattson and Bishoff s.n.* (IDF!). Adams Co.: Snake River Canyon, ca. 5 km s. of Hell's Canyon Dam, along Idaho Power Company right-of-way, 20 Apr 1977, *Meinke 1545* (OSC!).

Habitat. *Leptodactylon pungens* subsp. *hazeliae* occurs below 650 m, inhabiting rock walls and talus covered slopes. It has only been recorded from the deepest part of the Snake River Canyon, between latitudes 45° and 46°N, and is not known to be sympatric with any other species or subspecies of *Leptodactylon*. The vegetation in this area is dominated by *Poa sandbergii* Vasey, *Agropyron spicatum* (Pursh) Scribn. & Smith, *Purshia tridentata* (Pursh) DC., and *Celtis reticulata* Torr. Other endemic taxa occurring with subsp. *hazeliae* include *Rubus bartonianus* Peck, *Ribes cereum* Dougl. var. *colubrinum* Hitchc., *Phlox colubrina* Wherry & Const., *Astragalus cusickii* Gray, *A. vallis* Jones, *Nemophila kirtleyi* Hend., and *Hackelia hispida* (Gray) Johnst.

Floral phenology. Branch development is initiated in late February or early March, with flowering occurring from April through June. Inflorescences consist of one to three flowers [not strictly single-

TABLE 1. MORPHOLOGICAL COMPARISON BETWEEN *Leptodactylon pungens* (EXCLUDING SUBSP. *hazeltiae*), *L. pungens* SUBSP. *hazeltiae*, AND *L. watsonii*.

Characteristic	<i>L. pungens</i>		<i>L. watsonii</i>
	<i>L. pungens</i>	subsp. <i>hazeltiae</i>	
Habit	Usually erect, flowering stems woody	Sprawling to mounded, flowering stems herbaceous	Sprawling or loosely matted, flowering stems herbaceous
Leaf insertion	All alternate, or lower opposite and upper alternate	Lower leaves alternate and upper opposite	Strictly opposite
Leaflets	1-1.8 mm broad, stiff, linear-lanceolate or subulate	0.2-0.6 mm broad, soft-filiform	0.8-1.2 mm broad, stiff, linear-lanceolate
Calyx	6-11 mm long, the lobes equal or nearly so	8-13 mm long, the lobes slightly unequal	8-14 mm long, the lobes markedly unequal
Number of perianth parts	5	5(-6)	(5)-6
Number of flowers per inflorescence	(3)-5-9(-15)	1-3(-5)	1-5(-9)
Stem, leaf, and calyx pubescence	Densely glandular-tomentose, pubescent, or glabrate	Finely stipitate-glandular	Glandular-pubescent or occasionally glabrate

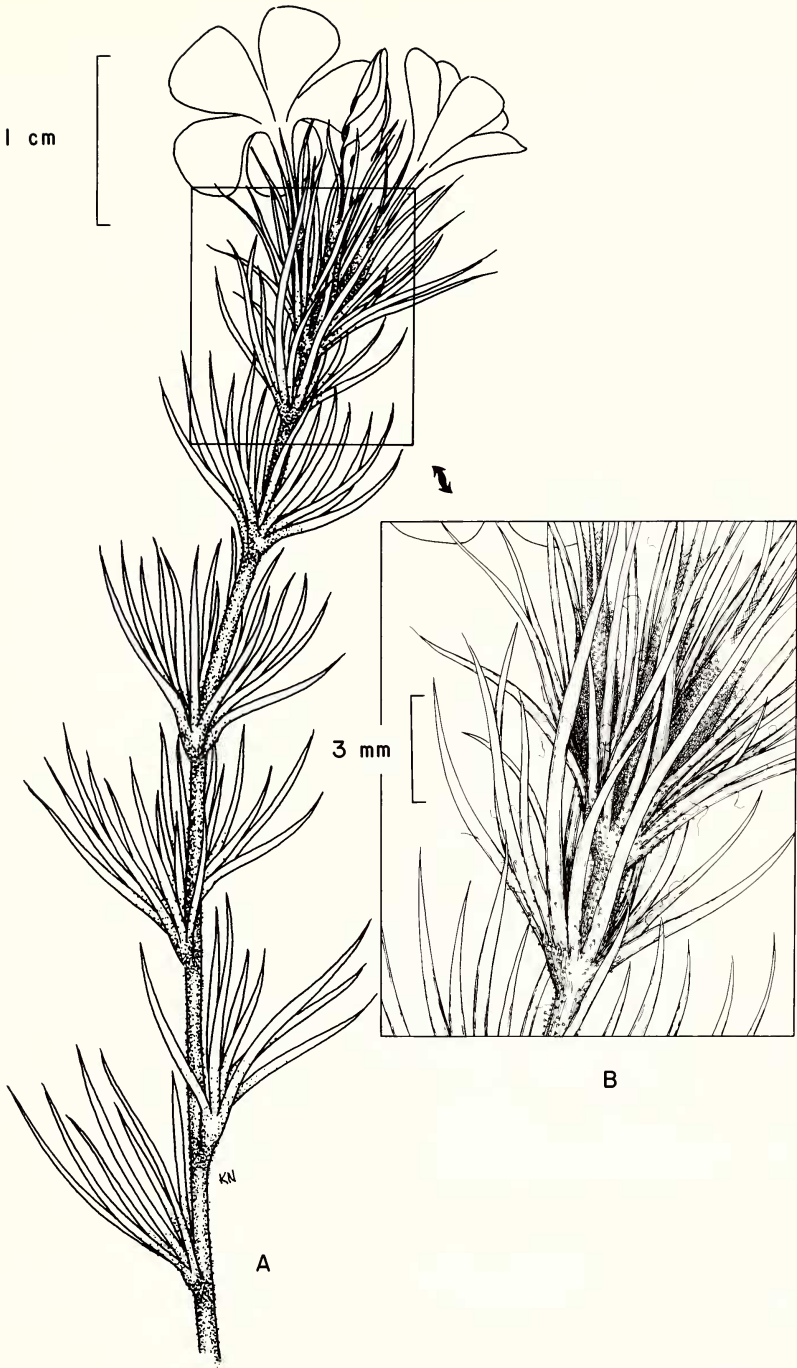


FIG. 1. *Leptodactylon pungens* subsp. *hazeliae*. A. Flowering stem. B. Enlargement illustrating the glandular stem, leaf, and calyx pubescence.

flowered as reported by Peck (1936, 1961)]. Corollas generally remain open throughout the day and produce copious nectar. Insect visitors are primarily pierid and lycaenid butterflies and (occasionally) sphingid moths. Capsules are tardily dehiscent and persistent, with seed dispersal occurring throughout the summer.

Relationships. The taxonomic relationship between subsp. *hazeliae* and its potential relatives is difficult to assess. By tradition, the possession of pentamerous flowers and at least some clearly alternate leaves implies affiliation with *L. pungens*. However, the sprawling habit, herbaceous flowering stems, and sparsely flowered inflorescences are suggestive of *L. watsonii* (Table 1). Moreover, the presence of 5-merous flowers is not unprecedented in *L. watsonii*, being known from a few scattered localities such as the Quinn Canyon Range of central Nevada (Cronquist 1984). The habit and stem traits also are shared by *L. glabrum* Patterson and Yoder-Williams, a recently described species that occurs at two sites in northwestern Nevada and southwestern Idaho. *Leptodactylon glabrum* is considered closely allied with *L. watsonii* because of its completely opposite phyllotaxy and strictly 6-merous flowers (Patterson and Yoder-Williams 1984). It is possible that subsp. *hazeliae* has a close affinity with *L. glabrum* because it is the only other intermountain congener with soft, filiform-linear leaflets less than 0.5 mm broad. Furthermore, subsp. *hazeliae* plants also, on occasion, possess a few 6-merous flowers. Both entities are apparently restricted to rocky habitats isolated in steep canyons, and neither are known to be sympatric with other members of the *L. pungens* or *L. watsonii* complexes. Although leaf insertion and the number of flower parts will generally discriminate the two taxa, there are distinctive pubescence differences as well. *Leptodactylon glabrum* is eglandular and often glabrous (Patterson and Yoder-Williams 1984), whereas *L. pungens* subsp. *hazeliae* is stipitate-glandular on the stems, leaves, and calyces (Fig. 1B). Many of the morphological characters that distinguish *L. glabrum* and subsp. *hazeliae* within the genus are intermediate between *L. watsonii* and *L. pungens*. This, coupled with their narrow geographic distributions, suggests that the two endemics could be remnants of past intergradations between *L. watsonii* and *L. pungens* in areas where these widespread species no longer coexist.

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